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COMMENTARY

Are crop yields limited by pollinators? Proper assessments using pollinator gradients require measurements of flower density and yield potential

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Abstract

1. It is widely documented that many crops depend on animal—and primarily insect—pollination, but the degree to which pollinators limit yield in comparison with other factors is poorly understood.
2. Recent studies conclude that pollinator visitation rates limit yields of many crops, based upon positive correlations between these two variables. However, these studies typically suffer from incomplete data on two key variables that affect both pollinator recruitment and yield: flower density per area and yield potential per flower, both driven by maternal resource availability.
3. Here we review the literature on animal-pollinated crops showing that (i) yields can be positively associated with flower density, and (ii) pollinator density can also be positively correlated with flower density; the third positive association observed between pollinator density and yield may result from the two first correlations, without causal relationship.
4. Likewise, positive associations observed between (i) the amount of maternal resources per flower and yield potential per flower, and (ii) between the amount of maternal resources per flower and pollinator density per flower can both explain the positive correlation observed between yield per flower and pollinator density per flower.
5. We conclude with an illustration reusing data from the literature to show that, without incorporating data on flower density and yield potential per flower, measuring yields and gradients of pollinator density per area alone can overestimate the degree to which pollinator visitation rates directly limit yield.

KEYWORDS
animal-pollinated crops, flower density, pollen supplementation, pollination deficit, pollinator density, pollinator gradient, pollinator limitation, yield potential

1 | INTRODUCTION

Recent studies report that yields of animal-pollinated crops are limited by pollinator visitation rates to flowers (or pollinator density per transect/area), for example, with Turo et al. (2024) showing that 28%–61% of these crops suffer from suboptimal pollinator visits globally (the range including model uncertainty). Inadequate pollinator activity also appears to limit fruit production for five of seven crops in the USA (Reilly et al., 2020a). These and similar other studies (e.g. Catarino et al., 2019; Garibaldi et al., 2013; Mallinger et al., 2021; Vezzani et al., 2025) relate crop pollination outcomes (such as number or mass of fruits or seeds per plant or area) to gradients of pollinator visitation rates to flowers counted along field transects, addressing the hypothesis that measures of pollination outcomes increase with pollinator visits per transect until a plateau is reached (Figure 1). This relationship can then be used to predict pollen limitation across fields based on observed pollinator densities (Figure 1; Reilly et al., 2020a; Turo et al., 2024; Vezzani et al., 2025). However, whether pollinator visits per se are driving pollination outcomes, and whether they can be used to infer pollen limitation, depend strongly on two additional but rarely measured confounding factors: flower density per transect and the yield potential per flower, both of which reflect maternal resource limitation (Boreux et al., 2013; Bos et al., 2007; Garratt et al., 2018; Harder & Aizen, 2010; Harder & Routley, 2006; Tamburini et al., 2019). Below we show how incorporating these two variables can modify the direct relationship between pollinator visitation rates and pollination outcomes, and argue that these need to be incorporated into future studies.

2 | FLOWER DENSITY

The number of flowers per plant or per unit area has been shown to vary both with cultivar and field for many crops, including highbush blueberry (*Vaccinium* spp.; Bozek, 2021; Cromie et al., 2024),

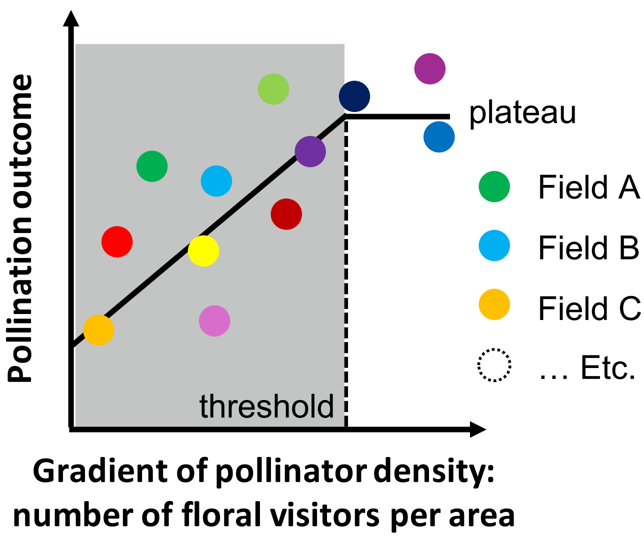

FIGURE 1 Proposed relationship between crop pollination outcome or yield (e.g. number or mass of fruits or seeds per plant or area) and pollinator density per transect or area. Crop pollination outcome increases linearly with pollinator density until a plateau is reached beyond a certain threshold of pollinator density. All the fields with measured pollinator densities below the threshold (located in the grey area) are considered to have a pollination deficit.

oilseed rape (*Brassica napus*; Carruthers et al., 2017), sunflower (*Helianthus annuus*; Palmer & Steer, 1985), coffee (*Coffea canephora*; Boreux et al., 2013), onion (*Allium cepa*; Hagler et al., 1990), carrot (*Daucus carota*; Koul et al., 1989) and squash (*Cucurbita pepo*; Milc et al., 2016). For sunflower, coffee and buckwheat (*Fagopyrum esculentum*), the number of flowers per plant is an important predictor of fruit or seed yield (Boreux et al., 2013; Chen et al., 2024; Palmer & Steer, 1985); furthermore, flower production per plant predicts yields of highbush blueberry and wild mustard (*Sinapis arvensis*) far better than pollinator visitation rates (Grant et al., 2021; Höfer et al., 2023). Additionally, flower density has been shown to be a key predictor of pollinator recruitment, especially for honey bees (*Apis mellifera*), with more foragers visiting plants or areas that offer more flowers (Bauer et al., 2017; Cromie et al., 2024; Höfer et al., 2023; Traine et al., 2026).

Because the densities of bees visiting crop flowers per area can be positively associated with flower density (Figure 2a), and pollination outcomes also often increase with flower density per area (Figure 2b), then the positive association found between pollination outcomes and pollinator density per area is not evidence of causation, but rather a correlation resulting from the two previous relationships (Figure 2c). Incorporating flower density may reveal that there is no longer a relationship between pollination outcomes and pollinator visitation rates when shown as pollination outcome per flower and pollinator visits per flower (Figure 2d). For this reason, it is essential for meaningful interpretations of pollinator limitation in crop pollination studies to include estimated densities of flower production per plant or unit area, and report both pollinator visits per count of flowers as well as pollination outcomes per count of flowers, for example, percentage fruit set (number of fruits/number of flowers) or yield per count of flowers (e.g. Mallinger et al., 2021).

While many studies investigating the relationship between pollinator density and pollination outcomes do incorporate flower density in fruit set measurements (83% of studies; Table S1), it is less commonly accounted for in other measurements of pollination outcomes (e.g. 13% of studies measured seed set per flower; 10% of studies measured fruit or seed yield per flower; Table S1) or in measurements of pollinator visitation rates (25% of studies; Table S1). Instead, many studies count the number of pollinators along transects or in a fixed area (i.e. quadrat), but most of the time without counting or standardizing floral units within these transects/areas. This is likely due to the challenge in counting the hundreds or even thousands of flowers available in even small units of area for the many crops presenting high flower densities (e.g. perennial crops, oilseed rape). Assessing flower densities at these scales may become more tractable in the future with advances in automatic image analyses (e.g. Farjon et al., 2020; Torresani et al., 2023). Another approach would be to estimate flower density at a larger scale by counting the number of flowers per branch or small area over repeated units, averaging and then multiplying by the number of branches per plant and plants per transect, or by total area observed (e.g. McGrady et al., 2020; Miñarro et al., 2023; see other examples in Table S1). On the other hand, for crops presenting low to moderate flower

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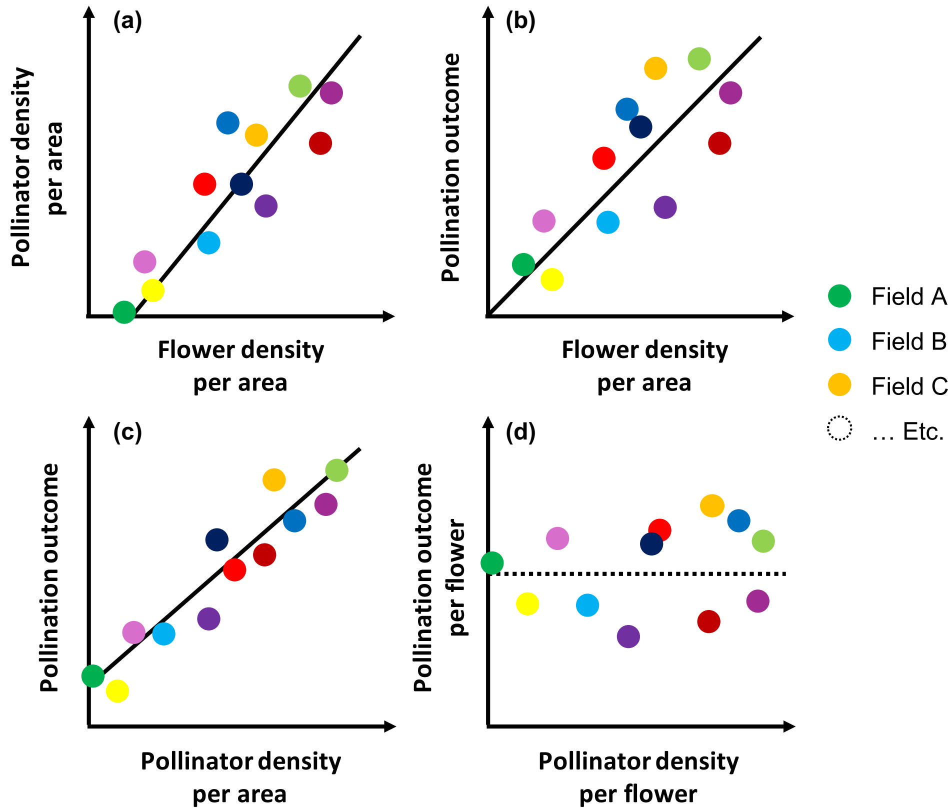

FIGURE 2 Positive relationships between pollinator density and flower density per area (a) and between pollination outcome and flower density per area (b), which are commonly observed across cropping systems, may both explain the positive correlation observed between pollination outcome and pollinator density per area (c). By incorporating flower density into measured variables, there may no longer be a relationship between pollination outcome and pollinator visitation rates when shown as pollination outcome per flower and pollinator visits per flower (d).

densities, counting the flower number can be directly feasible at the transect or observation area level (e.g. Cucurbitaceae; Petersen & Nault, 2014). Finally, an alternative approach is to standardize flower number by observing the same number of flowers across all transects (Garibaldi et al., 2016; Vaissière et al., 2011), or across stationary observation areas (Fijen & Kleijn, 2017; Garibaldi et al., 2020).

3 | MAXIMUM YIELD POTENTIAL PER FLOWER UNIT MEASURED WITH MANUAL POLLEN SUPPLEMENTATION

Even with similar flower densities, fields can present different maximum potentials of pollination outcomes or yields. Pollination outcomes are also limited by the pool of maternal resources available per plant to mature seeds and fruits from fertilized ovules and ovaries (Boreux et al., 2013; Bos et al., 2007; Garratt et al., 2018; Harder & Aizen, 2010; Harder & Routley, 2006; Tamburini et al., 2019). Consequently, assessing the maximum yield potential per flower unit with manual pollen supplementation is typically regarded as the best way to assess crop pollination deficits (Bos et al., 2007; Toledo-Hernández et al., 2020; Webber et al., 2020). Knowing maximum yield potential can inform interpretations of any correlations between pollinator visitation rates and pollination outcomes (e.g. Garibaldi et al., 2016), determining whether these are directly related to one another or both responding to a third factor—maternal resources (Figure 3)—just as was described above for flower density. For instance, Chabert et al. (2022) found that both sunflower seed number and mass per flower head were positively associated with pollinator densities per flower head across different fields (see Figure 3a). However, pollen supplementation showed that no field was pollen-limited. This illustrates that all fields reached their maximum yield potential per flower head, even those fields that received fewer pollinator visits per flower head. Furthermore, from these data, it was observed that the maximum yield potential per flower head was positively associated with pollinator density per flower head (Figure 3b), likely because both of these variables respond to maternal resource limitation (Chabert et al., 2022). Specifically, fields with higher maximum yield potential per flower head likely had more maternal resources available to plants, which could have in turn resulted in more florets per flower head or more nectar sugars produced per floret, traits that would result in more pollinator visits per flower head (Cromie et al., 2024; Mallinger & Prasifka, 2017; Prasifka et al., 2018) as well as a higher probability of fertilized ovules

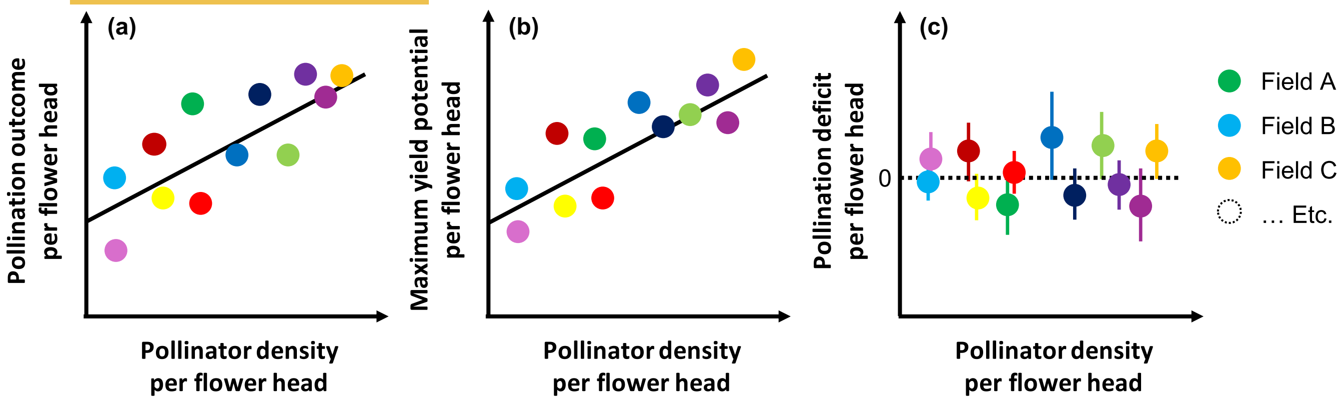

FIGURE 3 Positive relationships between pollination outcome and pollinator density per flower head (a) and between the maximum yield potential per flower head obtained through manual pollen supplementation and pollinator density per flower head (b). When maximum potential is used to calculate pollination deficits, there is no positive relationship observed between pollination deficit per flower head and pollinator density per flower head (c). Conceptual figures are based on the results obtained by Chabert et al. (2022). Error bars in (c) depict 95% confidence intervals overlapping with 0, showing no evidence of pollination deficit for any field.

developing into mature seeds. Thus, as with flower density, the positive relationship observed between pollinator visitation rate per flower unit and yield per flower unit could be the result of the positive relationships occurring between these two variables and a third variable, in this case, maternal resources dedicated to flowering and fruiting. Further in support of this conclusion, when maximum yield potential is used to calculate pollination deficits, there is no longer a positive relationship between pollination deficit per flower head and pollinator density per flower head (Figure 3c; Chabert et al., 2022).

Despite the importance of pollen supplementation to assess pollen limitation, only 22% of studies investigating the relationship between pollinator density and pollination outcomes include pollen supplementations to control for maximum yield potential (Table S1). Pollen limitation is best assessed by applying pollen supplementations at the whole plant scale (Knight et al., 2006; Webber et al., 2020; Wesselingh, 2007) as otherwise, resource reallocation among flowers within a plant can artificially enhance the magnitude of the measured pollination deficit. However, manually supplementing pollen can be especially tedious and labor-intensive for crop plants, many of which produce hundreds if not thousands of flowers per plant (Toledo-Hernández et al., 2020; Webber et al., 2020; Wesselingh, 2007). Thus, for practicability, pollen supplementations will often be applied at a lesser scale, such as a branch or raceme (Webber et al., 2020; Wesselingh, 2007). Manual pollen supplementations also require a number of conditions to be successful, including that the quantity and viability of pollen deposited is sufficient, that pollen is deposited when the pistil is receptive, and that deposition by hand does not damage the female organ as summarized in Young and Young (1992).

4 | ILLUSTRATION WITH DATA

The proportion of crop systems recently reported to be limited by pollinator visits (Reilly et al., 2020a; Turo et al., 2024) may be revised downwards once pollen supplementation data are included and variables are adjusted per flower or per count of flowers. For example, Turo et al. (2024) concluded that up to 86%, 55% and 100% of blueberry fields in British Columbia (BC), Michigan (MI) and Oregon (OR), respectively, were yield limited due to insufficient visitation by pollinators (Table 1). Using a similar approach, Reilly et al. (2020a) calculated that 94%, 72% and 64% of the transects measured in BC, MI and OR blueberry fields were pollinator limited. However, when Reilly et al. (2020a) included data with pollen supplementation to represent and adjust for the yield potential, there were only 88%, 42% and 22% of transects displaying pollinator limitation in these same fields (Table 1). Integrating pollen supplementation data generally reduced the frequency of calculated pollinator deficits. Had floral density also been measured and incorporated in their calculations, even fewer instance of pollinator deficits may likely have been found. Specifically, pollinator density was expressed in pollinators per transect and not per count of flowers, and the measured yields of fruits were not adjusted for differences among transects and fields in average flower production. Thus, any measured deficit in yield and/or in pollinator visitation rates may be due to low flower densities. For instance, using a different approach by incorporating maximum yield potential from pollen supplementations, and by accounting for the use of repeated transects within a field to address the likely variation in flower density at the field level, we calculated the mean ± 95% confidence interval (CI) of pollination deficits for each blueberry field reported in Reilly et al. (2020a) (Figure S1). By checking to see if the 95% CI overlapped or not with 0, we concluded that only 33%, 4% and 17% of the fields in BC, MI and OR, respectively, were pollen limited, significantly fewer than previously reported by Turo et al. (2024) (Table 1). However, because these calculations could only be made based on 3–4 repetitions (transects) per field, necessarily limiting the statistical power, 95% Cis are large. This limitation could thus lead to overestimating the number of fields in which the 95% CI overlaps with zero (e.g. fields of BC; Figure S1).

TABLE 1 Percentage of northern highbush blueberry fields or transects concluded to be yield limited (based on fruit mass per berry) due to lower than optimal pollinator visitation rates. Information retrieved from table S9 in Reilly et al. (2020a) and table S2 in Turo et al. (2024).

			Reilly et al. (2020a)		Turo et al. (2024)	Our calculations
			% of transects with pollinator deficit		% of fields with pollinator deficit	
State /province	Number of fields	Number of transects	Without pollen supplementation	With pollen supplementation	Without pollen supplementation	With pollen supplementation
British Columbia	45	177	94%	88%	86%[a]	33%[b]
Michigan	49	188	72%	42%	55%[a]	4%[b]
Oregon	12	45	64%	22%	100%[a]	17%[b]

[a]The percentages displayed result from calculations of the weighted average over years per state or province of the percentages of fields 'possibly pollinator limited' according to Turo et al. (2024).

[b]We calculated the mean ± 95% CI of pollination deficit of each field and deduced the percentage of fields with a significant pollination deficit. A field was considered to have a significant pollination deficit when the 95% CI did not overlap with 0 (see Figure S1). Pollination deficits were calculated from the difference of average fruit mass between pollen supplemented and open pollinated flowers. The samplings with open and supplemental pollinations were repeated within 3–4 transects per field (data provided in Reilly et al. (2020a, 2020b)), enabling the calculation of a 95% CI around the average pollination deficit for each field, with variation between transects.

5 | CONCLUSION

Lastly, other biotic or abiotic factors driving both pollinator densities and pollination outcomes per unit area may also explain the positive correlation observed between pollinator density and pollination outcomes. For instance, insect pollinators and natural enemies regulating crop pests are both positively correlated with landscape complexity (Holland et al., 2017; Shackelford et al., 2013), and yields may be driven by natural enemies and not by insect pollinators. Likewise, insect pollinator activity and pollen germination on stigmas both respond to temperature with a unimodal shape (Colinet et al., 2015; Tushabe & Rosbakh, 2025), meaning that pollination outcomes may be driven by pollen performance and not by insect pollinators under specific temperatures. A way to disentangle these potentially confounding factors is again to assess the yield potential in each climate or landscape context with manual pollen supplementations, and to relate the pollination deficit per flower to the pollinator density per flower.

AUTHOR CONTRIBUTIONS

Stan Chabert, Bernard E. Vaissière, Rachel E. Mallinger and James H. Cane conceived the commentary. Stan Chabert wrote the first draft, created the figures and tables and analysed the data. Rachel E. Mallinger, James H. Cane and Bernard E. Vaissière reviewed and edited the manuscript. All authors approved the manuscript in its final form.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data used in this commentary were retrieved from the manuscript of Reilly et al. (2020a): https://doi.org/10.1098/rspb.2020.0922 and are available in Reilly et al. (2020b): https://doi.org/10.5061/dryad.hdr7sqvfj.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Pollination deficit calculated from fruit mass per berry for each field within a given year per state or province.

Table S1. List of crop studies that investigated explicitly, with at least one figure presented in the core manuscript, the relationship between pollinator density and at least one pollination outcome.

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